

# Comparative Analysis of the Jamming Avoidance Response in African and South American Wave-Type Electric Fishes

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**Abstract.** African wave-type electric fish, *Gymnarchus*, and South American wave-type electric fish, *Eigenmannia*, have evolved electrosensory and electromotor systems independently. Nevertheless, they exhibit a similar electrical behavior, the jamming avoidance response (JAR). When two individuals with slightly different frequencies of electric organ discharge (EOD) meet, they shift discharge frequencies away from each other to avoid mutual jamming of their electrolocation systems. These two genera of electric fishes perform this behavior using an identical set of complex computational rules. Reflecting their independent evolution, however, neuronal implementation of the computational steps appears to take different forms. One of the essential computational steps, phase comparison, is performed in the hindbrain in *Gymnarchus* and in the midbrain in *Eigenmannia*. The comparison of these two species in this paper revealed an example of how different brain structures perform functionally similar tasks in independently evolved systems that have a similar overall behavioral function.

## Introduction

Weakly electric fishes generate a weak electric field on the order of millivolts per centimeter from their electric organ. The electric field envelops the fish, and the distortion of the electric field caused by environmental objects

is sensed by electroreceptors located all over its skin surface. This active electrolocation process helps the fish to locate and identify surrounding objects and prey (Bastian, 1986). As with detection mechanisms in other sensory modalities, the electrosensory system seems to employ temporal and spatial information for localizing and identifying objects. The complexity of the temporal and spatial analysis by central electrosensory mechanisms has been revealed in a particular electromotor behavior, the jamming avoidance response (JAR) (Heiligenberg, 1991). This behavior is not an electrolocation behavior *per se* but preserves electrolocation ability when the fish's own electric organ discharges (EODs) are jammed by those of a neighboring fish.

Similar JARs are known in remotely related electric fishes, *Gymnarchus* and *Eigenmannia* (Bullock *et al.*, 1975). *Gymnarchus* and *Eigenmannia* are wave-type electric fishes that emit EODs at constant, individually fixed frequencies (250–600 Hz). When two fish with similar discharge frequencies meet, however, their electrolocation systems jam each other, resulting in a partial loss of electrolocation ability. To avoid this jamming, the two fish shift their discharge frequencies in the direction that will increase the frequency difference, restoring their electrolocation ability. The fish decide whether they should increase or decrease their EOD frequency according to the *sign* of frequency difference between their own and the neighbor's EOD (Watanabe and Takeda, 1963; Bullock *et al.*, 1972, 1975).

*Gymnarchus*, an African mormyrid fish, and *Eigenmannia*, a South American gymnotiform fish, are distantly related electric fishes that lack common electroreceptive ancestors and appear to have evolved both electroreception and electrogenesis independently (Lauder and Liem, 1983). Therefore, these two genera provide a

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*Abbreviations:* EOD: electric organ discharge; ELL: electrosensory lateral line lobe; JAR: jamming avoidance response.

rare opportunity to study complex neuronal mechanisms in vertebrates that have independently evolved to perform a similar behavior. In this article I compare the JARs of *Gymnarchus* and *Eigenmannia* in terms of computational rules, physiology, and anatomy.

### Computational Rules

Despite their independent evolution, *Gymnarchus* (Kawasaki, 1993) and *Eigenmannia* (Heiligenberg *et al.*, 1978; Heiligenberg and Bastian, 1980) share a remarkably similar but complex set of computational rules for their JAR that has the following four major computational features.

The first shared feature is that the sign of the frequency differences is extracted from complex afferent information without referring to pacemaker signals internally. The pacemaker nucleus is the intrinsic neuronal oscillator in the medulla in which neurons fire in synchrony, producing command pulses that are sent to the electric organ and trigger individual EOD waves. Thus, the fish could compare the frequency of the pacemaker signal with that of a neighbor's discharge to obtain information about the sign of frequency difference between its own and the neighbor's discharge. The following experiment, however, eliminates this possibility. The fish's EOD was silenced by curare, and an external electrical signal that mimics the fish's natural EOD was applied to the fish. The frequency of the replacement signal could be arbitrarily set independent of the frequency of the pacemaker signal. EODs of a neighbor were mimicked by the second external signal. JAR was driven by the frequency difference between these two external signals regardless of the frequency relation between the pacemaker and the neighbor's signal, demonstrating that fish do not make internal reference to the pacemaker for the JAR (Heiligenberg *et al.*, 1978; Kawasaki, 1993).

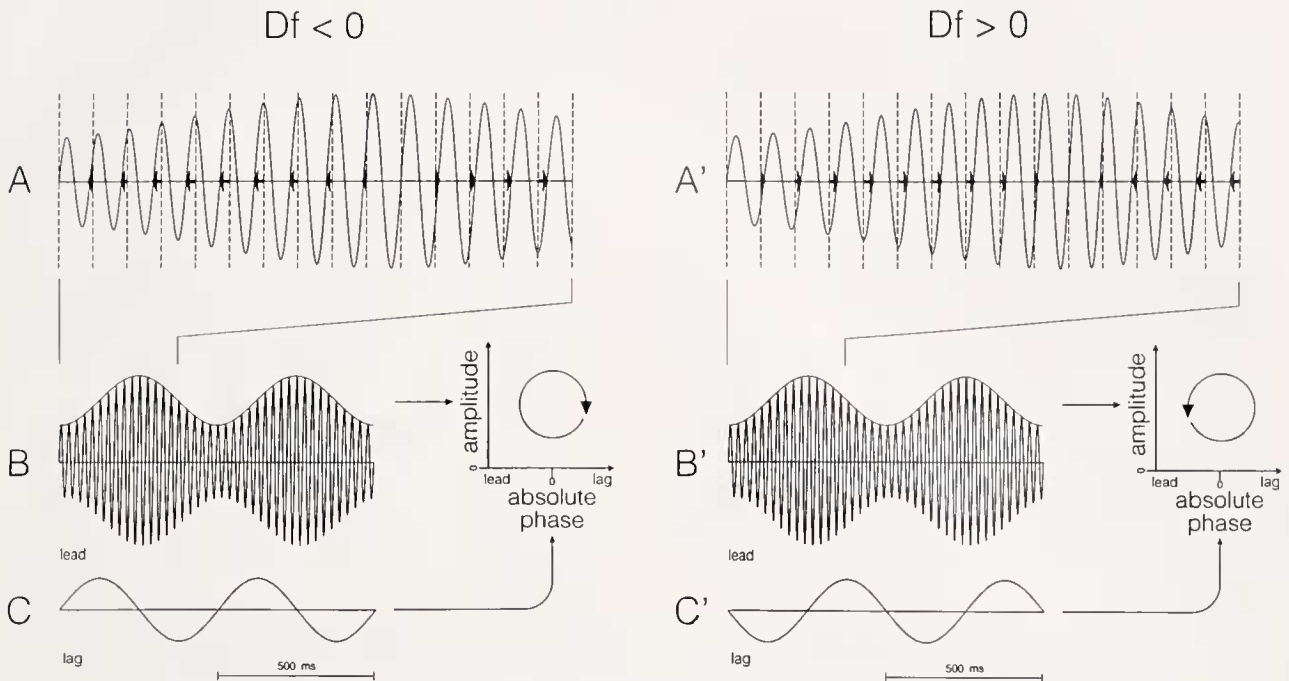
The lack of internal reference to the pacemaker in *Gymnarchus* is surprising because it belongs to the same family as *Gnathonemus*, a pulse-type African electric fish (Hopkins, 1986) that possesses the internal reference mechanisms. In *Gnathonemus*, the command nucleus in the medulla, which generates the EOD rhythm and drives the electric organ, sends a copy of the electromotor command, a corollary discharge, within the brain to the sensory systems in order to gate all afferent signals. Thus, exafference, the sensory input due to a stimulus caused by an external source, and reafference, a sensory input caused by the animal's own acts, are clearly distinguished by this neuronal hardware (Meyer and Bell, 1983; Bell, 1986a, b; Bell and Grant, 1989). The anatomical organization of the pacemaker nucleus of *Gymnarchus* is similar to that of *Gnathonemus* but lacks the cor-

ollary discharge projection. A projection from the pacemaker nucleus in *Gymnarchus*, which resembles the corollary discharge pathway in *Gnathonemus*, does not reach any sensory areas of the brain and solely projects back to the relay nucleus that drives the electric organ (Kawasaki, 1994).

The second computational feature found in both *Gymnarchus* and *Eigenmannia* is that the sign of the frequency difference between the fish's own EOD and the neighbor's EODs is computed from the temporal pattern of amplitude and phase modulation that is created in the summed signal of the two EODs. Each of the amplitude and phase modulations occurs at the *absolute* frequency difference between the fish's own and a neighbor's EOD and thus cannot encode the sign of the frequency difference. The temporal combination of them, however, uniquely encodes the sign of the frequency difference, and behavioral experiments demonstrate that fishes use this temporal pattern of amplitude and phase modulation for the JAR (Fig. 1) (Heiligenberg *et al.*, 1978; Kawasaki, 1993).

The third shared feature is the use of phase *difference* for computing the time course of phase modulation. Analysis of phase modulation requires a timing reference signal. The pacemaker signal, which is constant in phase, would be an ideal timing reference signal and could be compared for detecting phase modulation of the sensory signal. The first computational rule, however, eliminates this possibility. Instead, fish compute phase *difference* between different body areas to detect the time course of phase modulation (Fig. 2, left). Experimental elimination of the phase difference between body areas eliminates the JAR (Heiligenberg and Bastian, 1980; Kawasaki, 1993).

The last shared feature is the distributed analysis of sensory information. These fish always perform the JAR correctly—that is, they shift the EOD frequency in the direction that increases the frequency difference between two fish, regardless of the spatial orientation of the electric field by a neighbor. Any single computational component associated with a particular area of the body surface can encode the sign of the frequency difference only ambiguously, however, because the computation of phase difference inherently makes errors when the spatial orientation of a neighbor's electric field changes. The right panel of Figure 2 explains how differential phase computation errs in detecting the correct phase modulation. Although phase computation in each area may or may not provide correct information, it is differentially weighted by the size of the local amplitude modulation. Totalling such computational results from all body areas, the fish is always able to perform the JAR correctly (Heiligenberg and Bastian, 1980; Kawasaki, 1993). Neuronal mechanisms for this spatial integration of information remain to be explored.



**Figure 1.** Amplitude and phase modulation in the mixture of two sinusoidal signals mimicking the fish's own and a neighbor's EODs. The frequency difference is  $Df = -2$  Hz on the left panel and  $Df = +2$  Hz on the right panel. Amplitude, or envelope of the signal mixture (B and B'), shows sinusoidal modulation at 2 Hz. The first part of B and B' is expanded in time in A and A' to reveal the phase modulation. The phase leads that of the uncontaminated signal (vertical broken lines) during amplitude rises and lags during amplitude falls in A. In contrast, timing of zero-crossings lags during amplitude rises and leads during amplitude falls in A'. In C and C', zero-crossing timing of B in reference to that of the uncontaminated signal (absolute phase) is plotted. In the amplitude-phase plane (inserts), the amplitude (*i.e.*, the envelope of B and B') is plotted on the ordinate, and the absolute phase (C and C') is plotted on the abscissa. Due to unique temporal relations between amplitude and phase modulation for  $Df < 0$  and  $Df > 0$ , a circular graph rotates clockwise and counterclockwise for  $Df < 0$  and  $Df > 0$ , respectively. For graphical purposes, signal frequency is set at 40 Hz instead of the natural range of 250 to 600 Hz, and the amount of phase modulation, which is too small to be recognized in B, is exaggerated in A. (After Kawasaki, 1993.)

### Phase Comparison Mechanisms

It is remarkable that *Gymnarchus* and *Eigenmannia* have independently evolved the JAR with identical computational rules of this complexity. Because of their independent evolution, however, the physiological implementation of these computational steps is not necessarily expected to be identical. Although physiological mechanisms for the JAR in *Eigenmannia* are well analyzed (Bastian and Heiligenberg, 1980; Heiligenberg and Rose, 1985, 1986; Rose and Heiligenberg, 1986; Rose *et al.*, 1988; Kawasaki and Heiligenberg, 1990), analysis of those of *Gymnarchus* has only recently begun (Kawasaki and Guo, 1996). So far, comparison of the physiological mechanisms for the detection of phase difference is possible.

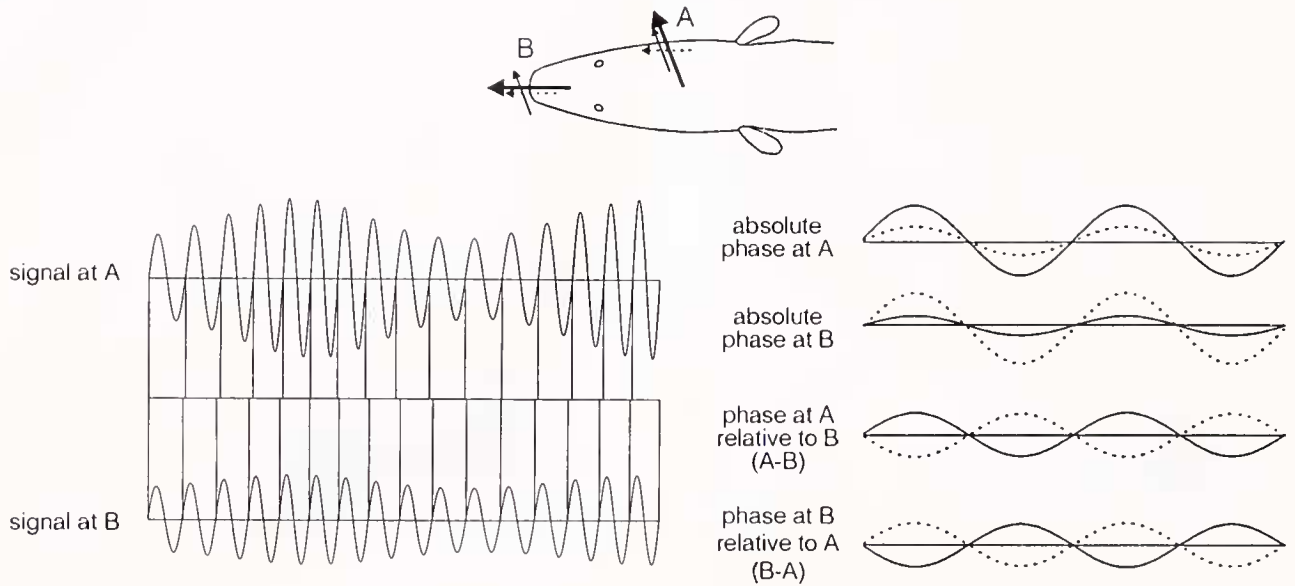
#### *Differential phase comparison in Gymnarchus*

Because *Gymnarchus* emits EOD at a constant frequency, the timing of zero-crossings, or phase, of electro-

sensory feedback of EODs at electroreceptors is constant when there is no neighboring fish. When a neighbor appears, however, electroreceptors are stimulated by the sum of the EODs of the fish and its neighbor; these modulate in phase as well as in amplitude at a frequency equal to the absolute frequency difference between the two fish (Fig. 1). Because of the geometrical difference between the fish's own electric field and that of the neighbor, the amplitude ratios between them are different at different locations on the body surface. This differential contamination results in a difference in the depth of phase modulation, which is a function of the ratio between the two signals (Fig. 2). This phase difference, one of the essential cues for the JAR, is detected by the following physiological mechanism.

The S-type tuberous receptor afferents fire one action potential at the zero-crossing of each stimulus cycle and thus encode phase by the timing of the action potentials. They project directly to the inner cell layer of the medial zone in the electrosensory lateral line lobe (ELL).





**Figure 2.** (Left) Phase differences between two body areas A and B. The fish's own electric organ discharge establishes a radial electric field (long arrows) because of the internal location of the electric organ, while the neighbor's EOD creates a more-or-less parallel field (short solid arrows) due to the external location of the neighbor's electric organ. Electroreceptors, which are sensitive to the local electric field oriented perpendicularly to the skin surface, are more-or-less evenly stimulated by the fish's own EOD across all body areas. The degree of stimulation by the neighbor's EOD, however, differs between areas A and B. The depth of phase modulation is a function of the ratio between the two signals; thus differential phase modulations arise between areas A and B. (After Kawasaki, 1993.) (Right) Differential phase computation may yield a wrong result depending on the spatial orientation of the neighbor's electric field. Two spatial orientations of the neighbor's electric field are assumed (short solid arrows and broken short arrows in left). The vertical axis represents absolute and relative phase modulations at areas A and B. The solid orientation yields a deeper phase modulation in A, and the dotted orientation yields a stronger modulation in B because of the different mixing ratios. Subtraction of the absolute phase at A from that of B, or *vice versa*, is shown in the bottom two traces. Note that the change of orientation results in the inversion of the sign of the phase difference. Note also that such a sign inversion of phase information implies the opposite sign of frequency difference between the fish's own and the neighbor's EOD as evident from Fig. 1.

Branches of these afferent fibers project also to the somata of giant cells in the medulla (Fig. 3). The giant neurons in turn project bilaterally to the inner cell layer of the ELL. Giant cells also fire one action potential for each stimulus cycle in response to the input afferent fibers. Thus, at the inner cell layer of the ELL, phases at different locations on the body surface are jointly represented by the timing of action potentials by S-type afferent fibers and giant cells. Neurons in the inner cell layer respond to phase *difference*.

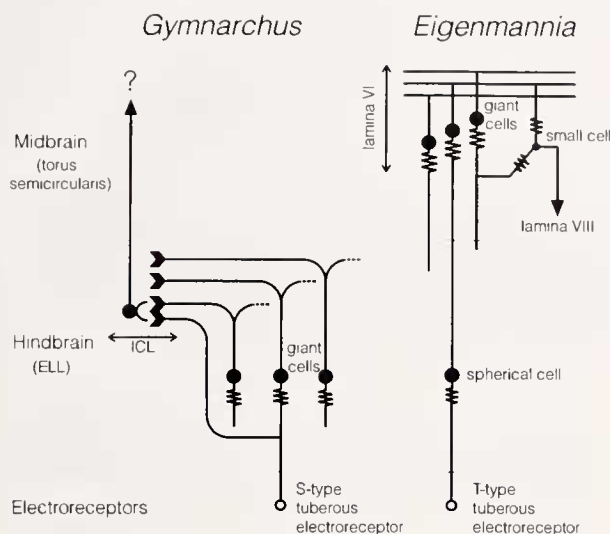
Figure 4 shows responses of differential-phase-sensitive neurons in the ELL recorded as extracellular potential. The fish was placed in a chamber in which the head and trunk portions of the body surface were electrically isolated for accurate control of phase difference between the two areas. When the phase of the head portion was modulated by  $\pm 70 \mu\text{s}$  at 1 Hz and the trunk portion was stimulated with an unmodulated signal with the same carrier frequency, the neurons responded to phase *advance* of the

head signal. When the stimuli in the head and the trunk were interchanged, the neuron responded to the phase delay of the trunk stimulus, demonstrating that the neuron responds to the phase difference between the head and trunk areas. Intracellular recordings and labeling revealed that these neurons project to the torus semicircularis in the midbrain (Kawasaki and Guo, 1996).

These differential-phase-sensitive neurons are sensitive to a phase difference in the microsecond range. Behavioral and physiological experiments demonstrate that *Eigenmannia* can resolve sub-microsecond phase differences, and corresponding neuronal sensitivities are found in central neurons (Rose and Heiligenberg, 1985; Kawasaki *et al.*, 1988). Behavioral thresholds for phase comparison have not been measured in *Gymnarchus*.

#### *Differential phase comparison in Eigenmannia*

Similarly to the S-type tuberous electroreceptors in *Gymnarchus*, T-type tuberous electroreceptors in *Eigen-*



**Figure 3.** Comparison of differential phase coding systems in *Gymnarchus* and *Eigenmannia*. S-type and T-type electroreceptor afferents, giant cells, and spherical cells fire an action potential for one stimulus cycle, thus encoding absolute phase at each electroreceptor organ. Neurons in the inner cell layer (ICL) in the ELL in *Gymnarchus* and small cells in lamina VI of the torus semicircularis in the midbrain in *Eigenmannia* receive such phase-locked inputs from different body areas and respond to the phase difference between them. The nature of the synapses in *Gymnarchus* is not known. Synapses represented by the resistor notation in *Eigenmannia* are of mixed type.

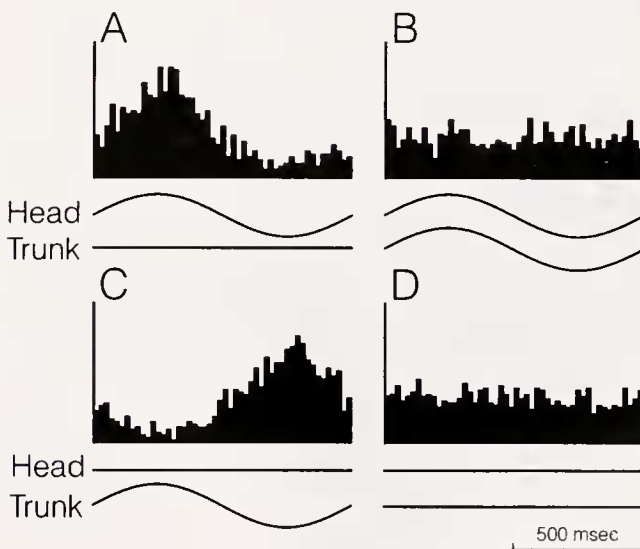
*mannia* fire one action potential for each stimulus cycle encoding phase information (Scheich *et al.*, 1973). Their sole projection is made to the somata of spherical cells in the ELL. The response of the spherical cells is also phase preserving, responding to each cycle of electrosensory stimulus by an action potential. Unlike in *Gymnarchus* in which the first central neurons, the giant cells in the ELL, bilaterally spread their axons for differential phase computation within the ELL, the spherical cells in *Eigenmannia* do not spread any processes within the ELL—they project single axons to lamina VI of the torus semicircularis in the midbrain. There they synapse onto the somata of the giant cells that then spread large axonal arbors for differential phase comparison. The small cells in the lamina VI receive inputs from the giant cells and the spherical cells and respond to the phase difference between these inputs (Fig. 3) (Carr *et al.*, 1982, 1986a, b; Heiligenberg and Rose, 1985).

### Comparative Implication

Thus, the function of differential phase comparison, one of the essential computational elements for the JAR, is assigned to different brain structures in *Gymnarchus* and *Eigenmannia*. Despite this difference, the internal organization of the phase comparison circuitry within

the structures is strikingly similar. In both systems, absolute phase information is supplied to phase-comparing neurons (neurons in the inner cell layer of the ELL in *Gymnarchus* and small cells in the lamina VI of the torus semicircularis in *Eigenmannia*) via two pathways—directly by phase coding afferent to the structure (S-type afferents in *Gymnarchus* and spherical cell afferents in *Eigenmannia*) and indirectly by adendritic giant cells with large axonal arbors. Also the differential-phase-sensitive neurons occur in a layered structure. The existence of similar phase-comparison circuits in different brain structures demonstrates that these fish indeed have developed this function by convergent evolution.

In *Gnathonemus*, which belongs to the same family (Mormyridae) as *Gymnarchus*, timing information of EOD pulses from neighboring fish appears to carry a species-specific or gender cue. The neighbor's EOD pulses are sampled by knollenorgan electroreceptors, and their afferent fibers project onto an adendritic soma of neurons in the nucleus of the ELL; this soma is reminiscent of the giant cells of *Gymnarchus*. Unlike the neurons in *Gymnarchus*, however, these neurons do not project within the ELL, they project to the midbrain (Szabo *et*



**Figure 4.** Extracellularly recorded single unit responses to phase difference in the ELL of *Gymnarchus*. Two traces below each histogram show the absolute phase of signals applied at the head and at the trunk part of an experimental chamber in which the curarized fish was placed for independent stimulation of these body areas (Kawasaki, 1993). (A) The trunk was stimulated with an unmodulated sinusoidal signal; the head was stimulated with a sinusoidal signal whose carrier frequency was identical but modulated in phase ( $\pm 70 \mu\text{s}$ ). The neuron showed a strong response to phase advance in the head. (B) The head and the trunk received identical stimuli which modulated in phase as in the head in A. (C) Stimuli in A were swapped between head and trunk. The neuron responds when phase at the trunk is delayed. (D) Both head and trunk received unmodulated sinusoidal signals. Note that B and D are similarly indifferent. (After Kawasaki and Guo, 1996.)

*al.*, 1975; Enger *et al.*, 1976; Mugnaini and Maler, 1987). Phase comparison appears to occur in the midbrain in this fish (Friedman and Hopkins, 1995).

The comparison of these differential phase circuits indicates that different brain structures may perform a similar function in independently evolved systems with similar overall function; conversely, homologous structures may not be assigned a similar function even in closely related species.

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